VIOLENT WAVE ACTION AND THE EXCLUSION OF EPHYDRIDAE (DIPTERA) FROM MARINE TEMPERATE INTERTIDAL AND FRESHWATER BEACH HABITATS

Bruce A. Steinly

Department of Entomology, University of Illinois, 320 Morrill Hall, 505 S. Goodwin, Urbana, Illinois 61801.

Abstract. —Evidence from a study of ephydrids in temperate habitats supports the hypothesis that insects are physically excluded from wave-disrupted marine and freshwater habitats (Buxton, 1926; Hinton, 1976a). Regularly flooded Scandinavian supralittoral (watt) and marine rock habitats and Lake Erie beaches exposed to violent wave action have the lowest shore-fly (Diptera: Ephydridae) richness. Marine and freshwater richness values increase with shore elevation and distance from disrupted beach habitats. A comparison of Scandinavian and Nearctic shore-fly communities with the Sorenson index of similarity indicates the resident populations were distinctive species assemblages. Behavioral avoidance, habitat preferences, and shortened developmental cycles presumably reduce immature mortality and exposure to periodic violent inundation.

Historically, insect competition with the Crustacea, osmoregulation problems, and periodic inundation have been considered the major constraints limiting insect colonization of marine habitats. In 1926, Buxton proposed that the physical violence of wave action excluded insects from intertidal areas. Hinton (1976a) reasserted that violent wave action has restricted insect colonization in marine habitats. Additionally, Hinton (1976b) suggested that violent wave turbulence, extreme, and rapid depth variations associated with regular flooding and drying have limited colonization of exposed intertidal zones. Although Buxton (1926) and Hinton (1976a, b) supported the wave action hypothesis, they did not present quantitative evidence substantiating their suppositions.

Beach and intertidal zones are submerged by periodic tides and/or occasional storms. During submersion and emersion episodes, beach and intertidal organisms experience fluctuating physical, chemical, and biological conditions. These conditions vary between the upper and lower limits of the intertidal range and are related to the magnitude of tidal fluctuation, duration, and wave action. The supralittoral (Neumann, 1976) division of the intertidal zone is irregularly flooded during storms and the marine tidal extremes of the equinoxes. The supralittoral fringe of the midlittoral is submerged every two weeks by the high waters of spring tides. The midlittoral is inundated by tides once or twice daily, and its sublittoral fringe is exposed only by the low waters of spring tides. The land-to-sea dimensions of these intertidal divisions depend on the amplitude of local tides and shore topography (Neumann, 1976).

Intertidal and freshwater beach habitat substratum characteristics are related to the degree of wind exposure, wave action intensity, and climatic factors (Neumann, 1976). Turbulent wave action associated with tides and storms severely disrupts the substratum. Commonly encountered disruptive processes include vertical mixing, horizontal displacement, erosion, and abrasion of substratum components.

Tidal and storm wave intensity is reduced significantly in sheltered marine environments. Sheltered environments include leeward coastal areas, bays, estuaries, lagoons, mangrove swamps, and saltmarshes. Saltmarshes, primarily confined to temperate regions, are expanses of herbs and shrubs periodically inundated by tides (Foster and Treherne, 1976). Saltmarshes form in areas sufficiently sheltered to allow the deposition and accumulation of fine inorganic and organic particulate matter (Teal and Teal, 1969). Although inundated periodically, the saltmarsh substratum is not severely disrupted, and, consequently, a variety of salt-tolerant plant species colonize the habitat. Saltmarsh habitats and niches are relatively stable compared to those in exposed intertidal zones. The greater insect abundance in saltmarshes suggests that salinity is a minor factor preventing insect colonization of the exposed intertidal zone (Hinton, 1976a). Neumann (1976) reported that salinity was not the limiting factor controlling intertidal vertical distribution of chironomids.

Several hundred insect species have colonized marine habitats (Cheng, 1976; Hinton, 1976a, b). The predominant proportion of colonizing insect species in marine habitats have originated in terrestrial rather than aquatic habitats. Hinton (1976a) considered aquatic and terrestrial environments to have comparable moisture levels. Submersion of terrestrial environments for prolonged periods is not a rare or isolated event (Hinton, 1976a). Hinton (1960) reported the more common presence of respiratory plastrons among terrestrial than aquatic insects.

A large majority of marine paurometabolous insects are found only in sheltered habitats (Table 1). Most water-strider species (Hemiptera: Gerridae) have invaded coastal water–bodies that have transient contact with the sea. These habitats include saltmarsh ditches and pools, brackish ponds and lakes, coastal rock pools, and brackish lagoons (Anderson and Polhemus, 1976). Additionally, gerrid species are found in estuaries, mangrove swamps, and sheltered bays (Anderson and Polhemus, 1976). The near-shore distribution of water-striders has been related to the degree of disturbance, water currents, wave action and wind exposure (Anderson and Polhemus, 1976).

Polhemus (1976) listed 20 species of Saldidae occurring in quiescent marine habitats and 8 species in the intertidal zone. In addition to the sheltered habitats listed in Table 1, saldids have been infrequently collected in mangrove swamps and beach-dune habitats. Species found in the intertidal zone are restricted to coral and rock reefs (Polhemus, 1976). Commonly, intertidal saldid species take refuge in volcanic rock pockets and crevices which reduce the risk of being swept out to sea by tidal currents. Uhler (1884) reported the retreat of *Pentacora signoreti* (Guerin) (Hemiptera: Saldidae) before the oncoming tide. Also, eleven species of intertidal (coral rock coast) *Halovelia* (Hemiptera: Veliidae) take refuge from wave action in holes of submerged rocks containing small pockets of air (Kellen, 1959).

Among holometabolous insects, the Diptera are most frequently collected in marine environments. Mosquito (Culicidae) adults and larvae are encountered

Table 1. Distribution of Marine Hemiptera.†

Family	Number of Species in Exposed Intertidal Zone	Number of Species in Sheltered Habitats*
Gerridae	0	54
Mesoveliidae	2	1
Veliidae	12	6
Saldidae	8	20
Gelastocoridae	1	2
Omaniidae	3	0
Total =	26	83

† Data extracted from Cheng, 1976.
* Sheltered habitats include: saltmarshes, estuaries, mangrove swamps, brackish pools above high tide mark, and leeward beaches.

primarily in mangrove swamps, saltmarshes, and brackish intertidal pools above the high tide mark (O'Meara, 1976). Approximately 100 mosquito species (Culicidae) have been identified from such sheltered marine environments.

Along the Atlantic and Gulf coasts of the United States, the larvae of no-see-ums (Ceratopogonidae) have been found in the intertidal zones of sheltered beaches (Goulding et al., 1953; Jamnback et al., 1958; Jamnback and Wall, 1958; Wall and Doane, 1960; Linley and Adams, 1972). Of the 60 marine ceratopogonid species, no species are known to occur where sand is subject to heavy wave action (Linley, 1976). Additionally, simulated wave action caused *Culicoides melleus* pupae to burrow more deeply into the substratum (Linley and Adams, 1972a; Dyce and Murray, 1967).

The non-biting midges (Chironomidae) have exhibited the greatest success in colonizing the marine littoral and sublittoral zones. In general, chironomid larvae have been found in various moss-like or felt-like filiform algae that thickly encrust rock or coral-reef substrata (Neumann, 1976). This association apparently is independent of algal species (Neumann, 1976). Many benthic marine midges construct a protective case in the algae (e.g. *Pontomyia* spp.).

In the exposed intertidal zone, adult midge activity may be interrupted by wind and heavy surf. The severity of weather and wave action has been mitigated by several unusual adaptations (Neumann, 1976). Those adaptations, discussed by Neumann (1976) include: synchronization of emergence time with calm weather or with benthic habitat exposure; dislocation of the swarming site to protected locations; short adult life (a few hours), so emergence, mating, and oviposition coincide with the exposure of intertidal habitat; resistance to submersion by wave action; oviposition behavior and the characteristics of the egg mass.

Only five Coelopidae species have been reported from marine beaches (Dobson, 1976). The seaweed (or kelp) flies (Coelopidae) utilize marine algae washed ashore into wrack rows by intensive wave action. Throughout the year, these transient rows of decaying plant material are used for food and shelter (Backlund, 1945). These wrack rows are usually removed within two to four weeks by storms or periodic high tides. Within the sheltering wrack, kelp flies complete development within 12 days (Dobson, 1976). This shortened life cycle enables the kelp fly to utilize a transient food supply and avoid severe wave action.

Table 2. Ephydridae (Diptera) found in aquatic habitats on Lake Erie shores.

Species	Sedge-Meadow		Marsh-Reed		Wave Zone Sand Beach		High Sand Beach		Limnic Wrack	
	Number N	Relative Abundance R.A.	Number N	Relative Abundance R.A.	Number N	Relative Abundance R.A.	Number N	Relative Abundance R.A.	Number N	Relative Abundance R.A.
Allotrichoma simplex	1	r					1	r		
Dichaeta caudata	1	r	2	r						
Discocerina obscurella	10	occ			4	r	3	occ	26	a
Ephydra riparia	27	a	1	r						
Hecamedoides glaucellus					35	c	58	va	30	a
Hydrellia crassipes			2	r						
Hydrellia griseola	8	occ							1	r
Hydrellia ischiaca			3	r						
Hydrellia tibialis	2	r								
Hydrochasma buccatum							1	r		
Hydrochasma leucoproctum					1	r	18	a	12	c
Lytogaster excavata			1	r						
Notiphila erythrocera			7	r						
Notiphila loewi							1	r		
Notiphila macrochaeta			1	r						
Notiphila pallidipalpis			1	r						
Notiphila scalaris			3	r						
Notiphila sicca			3	r						
Notiphila vittata	1	r								
Ochthera mantis	1	r	2	r						
Paracoenia bisetosa	2	r								
Paracoenia fumosalis	1	r								
Paralimna punctipennis			3	r						
Parydra breviceps	2	r	5	r						
Parydra quadrituberculata	14	occ	29	occ	2	r	1	r	2	r
Philygria debilis					3	r	3	occ		
Polytrichophora orbitalis	12	occ							4	occ
Scatella favillacea	78	va	176	va	95	va			1	r
Scatella obsoleta	9	occ	1	r	200	va	5	occ		
Scatella paludum	2	r	14	r	2	r				
Scatella stagnalis	9	occ	237	va	3	r	2	r	54	va
Setacera atrovirens			1	r						
Total	180		492		345		93		130	

Simpson (1976) listed 72 marine Nearctic shore-fly (Ephydridae) species. Approximately equal numbers of ephydrid species exhibited a preference for the exposed intertidal and quiescent marine environments. Although 22 species have been collected in intertidal areas, little information has been accumulated characterizing larval habitat requirements in North America.

In this paper, I review literature that suggests violent wave action influences the colonization and distribution of many marine and freshwater insects. Evidence is presented that suggests violent wave action is an additional constraint limiting the colonization of the Ephydridae (Diptera) in marine and freshwater lake habitats. The distribution of Scandinavian marine shore-fly communities are com-

Table 3. Species richness values (s) of ephydrid faunas in Scandinavian marine and Lake Erie aquatic habitats.

Marine Habitats	Species Richness (s)	Aquatic Habitats	Species Richness (s)
Watt (supralittoral)	5	Limnic wrack	8
Rock pool (supralittoral)	6	Wave zone-sand	9
Wrack	14	High sand beach	10
Marsh	13	Sedge-meadow	17
Grass pool	17	Marsh-reed	19
High sand beach	26		
Sand pool	20		
Hockenya	8		

pared with the Sorenson similarity index. Additionally, Nearctic ephydrid distribution, relative abundance, and similarity indices are described for quiescent and disturbed freshwater lake habitats.

Methods and Materials

Shore fly adults were collected with a modified aerial sweep net (Regensburg, 1977) and immediately killed with ethyl acetate at the site. Sampling was concentrated at Mentor Marsh and Geneva State Park in Ohio, and Presque Isle Park, Pennsylvania. Mentor Marsh and Geneva State Park marsh-reed and sedge-meadow habitats were contiguous with Lake Erie. These habitats in Ohio and Pennsylvania were characterized by vegetation types and/or substrate constitution (Steinly, 1978). The sedge-meadow (Weaver and Clements, 1938; Deonier, 1965; Scheiring and Foote, 1973; Regensburg, 1976; Steinly, 1978) was dominated by *Carex* Linnaeus species, *Juncus effusus* Linnaeus (common rush), *Glyceria striata* (Lamarck) A. S. Hitchcock (Manna grass), and *Scirpus cyperinus* (Linnaeus) Kunth. The marsh-reed habitat had large quantities of decaying plant debris floating on the water or associated with a moist substrate. The dominant macrophyte was *Typha latifolia* Linnaeus (broad-leaved cattail). The Scandinavian marine (Dahl, 1959) and Ohio aquatic (Scheiring and Foote, 1973; Steinly, 1978), 1984) limnic wrack beds consisted of varying quantities of wet decaying plant material washed onto maritime and lake shores, respectively. Repeated freezing and thawing during spring months uproot aquatic hydrophytes and strong wave action deposits leaves and stems on the shores.

The percent relative abundance (R.A.) of each species within the aquatic habitats was calculated. The percentage is equivalent to the number of a single species divided by the total number of ephydrids within the habitat. The result is multiplied by 100. The percentage ranges (Scheiring and Foote, 1973; Regensburg, 1976; Deonier and Regensburg, 1978; Steinly, 1978; Steinly and Deonier, 1980; Steinly, 1984) were characterized as follows: 1–2% rare (r); 3–8% occasional (occ); 9–14% common (c); 15–25% abundant (a); and 26–100% very abundant (va) (Table 2).

The ephydrid community composition of the marine Scandinavian supra-littoral (watt) and rock pool were compared by means of the Sorenson index of similarity (I) with all marine populations (Table 4). Shore fly population com-

Table 4.   Similarity of ephydrid faunas in Scandinavian marine habitats.

Marine Habitats	Index of Similarity (I)	
	Watt	Rock Pool
Watt[1]	—	—
Rock pool[2]	0.364	—
Wrack[3]	0.316	0.400
Marsh	0.555	0.316
Grass pool[4]	0.273	0.348
High sand beach	0.258	0.250
Sand pool[5]	0.240	0.462
Hockenya[6]	0.462	0.429

[1] Watt equivalent to supralittoral.
[2] Coastal rock pool adjacent to watt.
[3] Decaying rows of plant debris.
[4] Grass pool within marine marsh.
[5] Sand pool within high sand beach.
[6] Terrestrial zone farthest from supralittoral where topsoil largely independent of direct marine effects—permanent macrophytes.

position in all Scandinavian maritime habitats was reported by Dahl (1959). Additionally, the Sorenson index was utilized to compare shore fly populations in aquatic habitats located on the southeastern shore of Lake Erie (Table 5). The value of I ranges from 0 when there is no similarity (no species shared) between habitats to 1 when there is complete similarity (all species shared). The similarity index was calculated with the formula $I = 2C/A B$ where I is the index of similarity, C is the number of species shared, A is the number of species in habitat A, and B is the number of species in habitat B (Scheiring and Deonier, 1979). Ephydrid species numbers (richness values) in marine and freshwater habitats are listed in Table 3.

In Tables 4 and 5, marine and aquatic habitats are listed from frequently to infrequently inundated. The marine watt is inundated by tides and subjected to wave action daily while high sand beach and Hockenya are infrequently flooded by storms. Tidal inundation was negligible on the Lake Erie beaches, but these localities were subjected to extensive wave action when wind velocity was greater than 10 mph. All marine habitats had significant salinity levels; however, salt concentrations were thought to play a minor role as an ecological factor (Dahl, 1959; Hinton, 1976a).

RESULTS

The first comprehensive ecological and distributional investigation of the Ephy- dridae was accomplished in Scandinavia (Dahl, 1959). Of 68 shore fly species, Dahl recorded 41 species from marine habitats (biotopes). Of the 105 species in northern Ohio (Steinly and Deonier, 1980), 32 ephydrid species were collected in Lake Erie freshwater habitats (Table 2). Examination of habitat shore-fly com- munities reveals greater species richness (s) in stable Scandinavian marine and Lake Erie habitats (Table 3). The regularly flooded and severely disrupted marine watt (supra-littoral) had the lowest s while the infrequently inundated stable high sand beach yielded the greatest s value. Generally marine and freshwater s values increased with the distance above the supra-littoral.

Table 5. Similarity indices of Lake Erie aquatic habitats.

Habitats	Indices of Similarity		
	Wave Zone-Sand	High Sand Beach	Limnic Wrack
Wave zone-sand	—	—	—
Limnic wrack	0.706	0.555	—
High sand beach	0.736	—	—
Sedge-meadow	0.460	0.370	0.400
Marsh-reed	0.357	0.200	0.222

When marine shore fly communities were compared with the Sorenson index of similarity (I), the lowest I values were generated by the comparison of watt and rock pool to high sand beach. Also, the comparison of watt and rock pool with all marine habitats yielded low I values (Table 4).

The dominant species of Ephydridae in the Lake Erie sedge-meadow were *Scatella favillacea* Loew (va) and *Ephydra riparia* Fallén (a) (Table 2). *E. riparia* was rarely found in marsh-reed habitat. *Hecamedoides glaucellus* (Stenhammar) was collected from high sand beach (va), wave zone (c), and limnic wrack (a) habitats. Additionally, large numbers of *S. favillacea* (va) and *S. obsoleta* Loew (va) were found in the wave zone. Relatively few *S. obsoleta* (r) were collected in other freshwater habitats. *Hydrochasma leucoproctum* (Loew) (a) was dominant in the high sand beach habitat. The dominant shore-fly species in limnic wrack included *S. stagnalis* (Fallén) (va) and *Discocerina obscurella* (Fallén) (a). Large numbers of *S. favillacea* (va) and *S. stagnalis* were collected in the marsh-reed habitat.

The five aquatic Lake Erie habitats were compared with the Sorenson index of similarity (Table 5). The wave zone, high sand beach, and limnic wrack habitats had the greatest similarity. The comparison of sedge-meadow and marsh-reed to wave zone, high sand beach and limnic wrack ephydrid assemblages generated similarity values less than 0.460. Although the habitats within freshwater lake and marine ecosystems were located in close proximity to one another, the relatively low I values suggest that indigenous shore-fly communities were distinct species assemblages. Only the comparison of aquatic wave zone to high sand beach and limnic wrack yielded high indices of similarity.

DISCUSSION

During periodic storms, Scandinavian marine and Lake Erie beaches are subjected to intensive wave action. Additionally, marine beaches are exposed to varying degrees of wave action that depended on daily tides and wind velocity. The severity of substrate disruption has a significant impact on ephydrid nutrient and oviposition resources. Scheiring (1975) proposed that vegetation amount present during the year, the amount of organic debris and species utilizing the organic material, vegetation present at various times of the year, the length of time the vegetation was present and the dominant vegetation species were important habitat resources. Clearly, these nutrient and oviposition resources are disrupted by the physical impact of wave action. In an analysis of Iowa and northeast Ohio lotic habitat characteristics, Scheiring and Deonier (1982) found

shore fly richness variation was accounted for by the abundance and type of vegetation, presence of running water, and frequency of inundation. In all probability, the types and abundance of macroflora and microorganisms found on Lake Erie and marine beaches are limited by severity and frequency of violent inundation. Also, the intensity and frequency of inundation has a direct effect on the survival of ephydrid immature stages. Barton and Hynes (1978a) reported the elimination of wave-zone benthic macroinvertebrate communities by storms. Additionally, Barton and Hynes (1978b) reported that the variety and relative abundance of invertebrates on the exposed shores of the Laurentian Great Lakes were related directly to substratum stability. At more sheltered sites, Evans (1982) observed decreases in micrometazoan densities with depth above (+1 meter) and below (−1 meter) the Lake Erie wave zone. The reverse trend (increasing densities with increasing depth) was found in all wave-zone sites and was attributed to stress imposed on the fauna by wave induced sand-grain movement.

Although Ohio and Iowa lotic habitats have relatively high richness values (s) (Scheiring and Deonier, 1982), Scandinavian marine (Dahl, 1959) and Erie beaches have low s values. Iowa and northeastern Ohio lotic habitats have substrates that retain moisture (Scheiring and Deonier, 1982) while Scandinavian and Lake Erie beaches dry rapidly. Beach habitat (sand and/or rock) substrate is well drained and subject to solar and wind desiccation. In all probability, the movement of substrate and xeric beach conditions precluded the colonization of diverse and abundant macroflora and shore-fly assemblages.

Shore-fly relative abundance values suggest that several species are adapted to the indigenous physical and biological conditions peculiar to Lake Erie habitats (Table 2). *Scatella obsoleta, S. stagnalis, Ephydra riparia, Hydrochasma leucoproctum,* and *Discocerina obscurella* were found in large numbers in the wave zone, marsh-reed, sedge-meadow, high sand beach, and limnic wrack, respectively.

The total number of marine species confirms that the majority of Scandinavian shore flies are capable of utilizing saline habitats. The distribution of ephydrid species richness-values suggests that frequency and intensity of inundation has a major ecological impact. Scheiring and Deonier (1979) believed resource quantity increased the richness and abundance of well adapted ephydrid species in transient habitats.

In the watt and rock-pool habitats, herbivorous ephydrids had only a few algal species available (Dahl, 1959). Scheiring (1974) analyzed aquatic ephydrid species diversity and evenness in relation to habitat stability and available larval food. Scheiring (1974) and Deonier (1965) concluded that shore-fly larval adaptations are more important than those of adults in the determination of habitat distribution. Simpson (1976) noted marine shore fly larvae required relatively quiescent habitats, where the immature stages were protected from appreciable water movement. Scandinavian marshes were dominated by thick-growing macrophytes and algal populations (Dahl, 1959). Significant quantities of undisturbed organic debris provided ample substrate for micro-organism proliferation. Also, freshwater (= limnic) wrack, composed of decaying organic matter, provided a substrate for micro-organism growth (Scheiring and Foote, 1973). Although the marine wrack habitat is transient, the habitat may provide substantial larval and adult food resources for rapidly developing ephydrid species. Steinly and Runyan (1979) reported rearing the larvae of *Hecamede albicans* (Meigen) on marine mussels

commonly encountered in marine wrack rows. *H. albicans*, utilizing a transient habitat and food supply in the intertidal zone, completed development within ten to fifteen days (Steinly, unpubl.). Also kelp fly species (Dobson, 1976) utilized decaying vegetation in marine wrack. In all probability, kelp flies and *H. albicans* avoid periodic supra-littoral inundation, and the disruption of nutrient resources with a shortened life cycle. *Scatella picea* (Walker) and *Scatella stagnalis* (Fallén), freshwater shore flies encountered in ephemeral mud-shore habitat, have shortened life cycles (Connell and Scheiring, 1982; Foote, 1979). Rapid ephydrid development, a temporal adaptation, allows these species to avoid wave action and/or rapid stream flow associated with storms in marine and freshwater habitats, respectively.

Scandinavian marine grass pool have substantial accumulations of plant fragments and a rich grass vegetation surrounding and within the depressions (Dahl, 1959). The maritime high sand beach has diverse macrophyte and micro-organism populations. Species of diatom, chlorophyte, cyanophyte algae, and bacteria were commonly found by Dahl (1959). Marine sand-pool habitat had no permanent macrophytic vegetation but was bordered by highly productive algae populations (Dahl, 1959). These relatively stable habitats were infrequently inundated and were populated by a diverse and/or abundant micro-flora. Stable habitat substratum and nutrient resources probably have a significant influence on increased ephydrid s values.

The data compiled in Table 1 and the text suggest that more than half of the marine insect species are confined exclusively to sheltered habitats. In all probability, quiescent marine and freshwater habitats provide a refuge from severe wave action. In particular, saltmarsh, grass pool, marine high sand beach, sand pool, marsh-reed, and sedge-meadow insects have available a greater number of stable niches and nutrient sources.

Habitat preferences of marine and lake shore insects and behavioral and temporal adaptations of intertidal insect species substantiates the importance of avoiding intensive wave action. Additionally, the species richness distribution patterns, similarity, and relative abundance indices associated with Scandinavian marine and/or Lake Erie ephydrid populations support the wave disruption theory.

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